

**RESURRECTION OF *HIMANTURA OXYRHYNCHA*
(SAUVAGE, 1878) FROM THE SYNONYMY OF *H. UARNAK*,
A SENIOR SYNONYM OF *H. KREMPFI* (CHABANAUD, 1923)
(MYLIOBATIFORMES: DASYATIDAE)**

by

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ABSTRACT. Re-examination of the holotype of *Trygon (Himantura) oxyrhynchus* Sauvage (MNHN 9639) revealed that it is a species distinct from *Himantura uarnak* (Forsskål), and a senior synonym of *H. krempfi* (Chabanaud). Comparisons of the coloration, morphological variations and dermal armature of *T. oxyrhynchus* and the closely related species *Himantura uarnak* and *H. krempfi* show that *T. oxyrhynchus* is a valid species, re-named *Himantura oxyrhyncha* (Sauvage), and that *H. krempfi* could be a juvenile form of *T. oxyrhynchus* and, thus, a junior synonym. Moreover, the study of MNHN specimens of the *H. uarnak* complex has shown that some of them could be related to a new species, *Himantura* sp. A *sensu* Last & Stevens, 1987; and this species can be differentiated from the other *H. uarnak* specimens by the number of pectoral radials, morphological characters and coloration.

RÉSUMÉ. Validité d'*Himantura oxyrhyncha* (Sauvage, 1878) et commentaires sur la position taxinomique d'*H. krempfi* (Chabanaud, 1923) (Myliobatiformes: Dasyatidae).

Un nouvel examen de l'holotype de *Trygon (Himantura) oxyrhynchus* Sauvage (MNHN 9639) a montré que cette espèce était distincte du complexe d'espèces apparentées à *Himantura uarnak* (Forsskål) et qu'elle était le synonyme prioritaire d'*Himantura krempfi* (Chabanaud). Les comparaisons de la coloration, des variations morphologiques et du revêtement cutané de *T. oxyrhynchus* et des espèces apparentées *Himantura uarnak* et *H. krempfi* montrent que *T. oxyrhynchus* est une espèce valide, ici nommée *H. oxyrhyncha* (Sauvage), et que *H. krempfi* pourrait être la forme juvénile de *T. oxyrhynchus* et donc un synonyme de cette espèce. De plus, l'étude de spécimens MNHN du complexe *H. uarnak* a montré que certains d'entre-eux pourraient être rapportés à la nouvelle espèce *Himantura* sp. A *sensu* Last & Stevens, 1987 et que cette dernière peut être différenciée des autres spécimens du complexe *H. uarnak* par le nombre de rayons pectoraux, les caractères morphologiques et la coloration.

Key words. Dasyatidae - *Himantura oxyrhyncha* - *Himantura krempfi* - Synonymy - Taxonomy - Morphometry.

Sauvage (1878) described a new species of stingray, *Trygon (Himantura) oxyrhynchus*, from Saigon, Cochinchine (= Cambodia), based on a single female specimen. Garman (1913) considered this species synonymous with *Dasybatus* (= *Himantura*) *uarnak* (Forsskål, 1775), and his decision was accepted by Bertin (1939), Herre (1953), Compagno and Roberts (1982), Kottelat (1984), Séret and McEachran (1986) and Eschmeyer (1998), without any

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formal demonstration of arguments.

Kottelat (1984) was the first author to consider *T. oxyrhynchus* as a valid species. Later, Kottelat and Whitten (1996) mentioned *H. oxyrhynchus* from Borneo and Sumatra and considered this species synonymous with *H. krempfi*, based on Compagno and Roberts's work (1982). Eventually, Eschmeyer (1998) considered *T. oxyrhynchus* synonymous with *H. uarnak*, following Compagno and Roberts (1982) and Kottelat (1984). Recent publications concern only the presence of this species in different areas (Compagno, 1997; Wongrat, 1998; Froese and Pauly, 2000) or are mentioned in general checklists (Compagno, 1999).

However, Deynat (1995) has remarked that the coloration and some characteristics of the dermal armature of the *T. oxyrhynchus* holotype do not agree with those of *H. uarnak* specimens, but are similar to those observed in *H. krempfi*. The objective of the present study is to re-examine the status of *T. oxyrhynchus*, based on comparing morphology, dermal armature and coloration of this species with the closely related *H. krempfi* and the *H. uarnak* species complex (Last and Manjaji, pers. comm., 2001).

MATERIALS AND METHODS

Holotype. *Himantura oxyrhyncha* (previously identified as *H. uarnak*): MNHN 9639, immature female, 248 mm DW, Saigon, Cochinchine (Cambodia, Vietnam), coll. J. Julien. *Trygon (Himantura) oxyrhynchus* Sauvage, 1878, *Bull. Soc. Philomath.*, Paris, 7(2): 91.

Other specimens. *Himantura* cf. *oxyrhyncha* (previously identified as *H. krempfi*): MNHN 1923-71, immature female, 345 mm DW, Pnom Penh, Cambodia. Specimen given by the Professor Gruvel, Résidence Française au Cambodge, determined by Chabanaud (1923b); MNHN 1986-716, immature male, 185 mm DW, Mekong River (Cambodia), coll. d'Aubenton.

Comparative material. *Himantura krempfi* (Chabanaud, 1923), 3 specimens: MNHN 1922-78, juvenile male, 90 mm DW; MNHN 1922-79, juvenile female, 120 mm DW; MNHN 1922-77, juvenile male, 137 mm DW (140 mm DW in the original description), syntypes of *Dasybatus (Himanturus) krempfi* Chabanaud, 1923, Pnom Penh (Cambodia). *Himantura uarnak* (Forsskal, 1775), 7 specimens: MNHN 2442, juvenile female, 347 mm DW, New Guinea; MNHN 1985-208, juvenile male, 90 mm DW, Madagascar; MNHN A8909, 2 spms, 172 mm DW (juvenile female) and 184 mm DW (juvenile male), India; MNHN A7918, juvenile male, 312 mm DW, Vietnam; MNHN A7920, adult female, 422 mm DW, India; MNHN A7921, juvenile male, 220 mm DW, Indonesia; MNHN A7969, adult female, 374 mm DW, Red Sea; MNHN A8006, juvenile male, 300 mm DW, Indonesia.

Himantura uarnak is considered as a species complex, but is analysed herein under the name *H. uarnak* until more complementary information (Last and Manjaji, pers. comm.).

Measurements and counts

Measurements and meristic counts of specimens were made according to Wallace (1967) and Compagno and Roberts (1982). Morphometric measurements are expressed as percentage of disc width (DW) and are made point to point from the tip of the snout to the origin of the described structure, except for fin measurements expressed as length of the anterior and posterior parts. Counts of radial cartilages and vertebrae were made from radiographs, according to Compagno and Roberts (1982). Vertebrae were counted from the posterior edge of the second synarcual to the front edge of the pelvic girdle (synarcual-pelvic count) and to

the base of the sting (total count). Count of tooth rows was made according to Stehmann (1987). Terminology follows Deynat and Séret (1996).

Statistical analysis

To determine which variables were more suitable to separate the specimens, we performed a “log shape ratio” analysis (Mosiman and James, 1979; Darroch and Mosimann, 1985; Yoccoz, 1993), and we performed a double centered Principal Component Analysis (PCA) on log transformed data. However, this analysis take into account and remove isometric size. Because of the different size of the specimens, allometric variations were expected. To look at the allometric effect, we have plotted the different log-transformed variables, then, the different canonical axes with the size axis were calculated with the mean of all variables for each fish. The differences between species were tested using analysis of covariance. Abbreviations used in this study are explained in table I.

HIMANTURA OXYRHYNCHA (SAUVAGE, 1878)

Trygon (Himanturus) oxyrhynchus Sauvage, 1878: 91.

Trygon (Himanturus) oxyrhynchus: Kottelat, 1984.

Dasybatus (Himantura) uarnak: Garman, 1913; Bertin, 1939.

Himantura uarnak (synonym): Compagno and Roberts, 1982; Kottelat, 1984; Séret and McEachran, 1986; Eschmeyer, 1998.

Dasybatus (Himanturus) krempfi: Chabanaud, 1923a: 47, fig. 1 (three types, 90–140 mm DW, type locality, Pnom Pehn, Cambodia); Chabanaud, 1923b: 558–559 (reference and description); Chabanaud, 1926a: 6 (reference); Chabanaud, 1926b: 6 (listed).

Dasyatis krempfi: Fowler, 1930: 504 (reference); Fowler, 1941: 411 (description after Chabanaud, references).

Dasyatis (Himantura) krempfi: Fowler, 1969: 186 (listed; see discussion in Compagno and Roberts, 1982).

Himantura krempfi (Chabanaud, 1923): Monkolprasit and Roberts, 1990: 203; Kottelat and Whitten, 1996 (mistake following Compagno and Roberts, 1982).

Dasyatis bleekeri Smith, 1945: 42, pl. 1.

Himantura oxyrhynchus: Kottelat, 1984; Kottelat and Whitten, 1996 (cited); Compagno, 1997; Wongrat, 1998 (cited).

Himantura oxyrhyncha: Compagno, 1999.

Diagnosis

Himantura oxyrhyncha is consistent with the characteristics of the genus in presenting a tail much longer than disc length and in lacking skin folds on its ridges (McEachran and Capapé, 1984). It is characterised by the following combination of characters: disc quadrangular, snout elongate, dorsal surface of the disc with a reticulated color pattern, close-set dermal denticles with a flat heart-shaped crown, numerous heart-shaped tubercles with flat crown, extending from the nuchal area to the base of the sting.

Description

Morphometric ratios and meristics are presented in tables I and II. Values in brackets are related to the two other specimens of *Himantura* cf. *oxyrhyncha*. Disc longer than broad. Preorbital length 2.4 (2.2 – 2.6) times interorbital width. Preoral length 3.2 (3.2 – 3.3) times

Table 1. Measurements for *Trygon (Himantura) oxyrhynchus* (n = 13), *Himantura cf. oxyrhyncha* (n = 13), *Himantura krempfi* (n = 13) and *Himantura uarnak* species complex (n = 13). Measurement values are expressed as percentage of disc width (%DW).

	<i>H. oxyrhyncha</i> Holotype MNHN 9639	<i>H. cf. oxyrhyncha</i> MNHN 1923-71 (broken tail)	<i>H. cf. oxyrhyncha</i> MNHN 1986-716	<i>H. krempfi</i> Syntype MNHN 1922-79	<i>H. krempfi</i> Syntype MNHN 1922-77	<i>H. krempfi</i> Syntype MNHN 1922-78 (broken tail)
Total length (TL)	436.3	356.5	445.0	446.0	468.0	408.0
Disc length (DL)	114.5	117.7	113.6	115.0	113.0	115.0
Eyeball (Eb)	4.4	5.0	4.1	6.6	5.8	7.4
Interorbital width (IOW)	12.0	12.2	13.6	13.3	14.6	14.8
Internarial width (INW)	10.0	9.8	9.4	10.0	11.6	11.4
Mouth width (MW)	9.6	9.4	9.9	10.8	13.0	11.5
1st gill slit (GS1)	3.2	3.6	3.1	3.3	3.0	3.9
5th gill slit (GS5)	2.0	2.6	2.0	2.5	2.0	2.3
Width between 1st gill slits (GSW1)	22.6	22.2	21.9	22.5	23.3	24.2
Width between 5th gill slits (GSW2)	19.3	16.4	16.7	16.6	16.0	17.7
Snout tip to eye (SnE)	34.2	32.2	30.3	32.5	31.3	30.4
Snout tip to nostril (SnN)	28.2	26.7	26.7	28.3	27.7	25.3
Snout tip to mouth (SnM)	32.2	32.0	31.9	34.0	33.5	32.1
Snout tip to 1st gill slit (SnGS1)	44.7	44.7	45.0	47.5	43.0	44.2
Snout tip to 5th gill slit (SnGS5)	57.6	57.6	52.3	62.5	58.3	61.5
Snout tip to pelvic fin (SnPF)	93.5	96.8	91.6	96.0	91.2	97.4
Snout tip to vent (SnVF)	96.7	99.5	91.0	99.0	93.4	99.1
Pectoral fin anterior margin (PFa)	53.6	66.2	53.4	62.5	66.4	68.0
Pectoral fin posterior margin (PFp)	86.7	81.2	87.9	81.0	80.3	83.6
Tail base width (TaW)	8.4	9.1	8.3	11.0	11.0	11.5
Tail length (TaL)	333.9	263.7	336.7	331.5	346.9	287.4

Table I. – (Continued)

	<i>H. uarnak</i> MNHN 2442	<i>H. uarnak</i> MNHN 1985-208	<i>H. uarnak</i> MNHN A8006	<i>H. uarnak</i> MNHN A8909	<i>H. uarnak</i> MNHN A8909	<i>H. uarnak</i> MNHN A7918	<i>H. uarnak</i> MNHN A7920	<i>H. uarnak</i> MNHN A7921	<i>H. uarnak</i> MNHN A7969 (broken tail)
Total length (TL)	347.2	328.8	356.6	366.2	345.1	388.0	346.0	348.6	256.1
Disc length (DL)	91.6	91.1	94.0	89.5	88.6	85.3	93.3	83.6	89.8
Eyeball (Eb)	5.4	8.1	5.6	7.5	7.0	7.2	5.3	5.6	5.7
Interorbital width (IOW)	12.6	16.6	13.0	11.0	13.0	13.2	11.3	11.9	13.6
Internarial width (INW)	8.0	8.7	7.6	8.3	8.7	8.9	7.3	9.0	8.8
Mouth width (MW)	8.3	9.1	7.6	7.6	8.1	9.3	7.9	7.5	8.2
1st gill slit (GS1)	2.3	3.5	3.0	2.6	3.0	2.5	2.8	2.8	2.9
5th gill slit (GS5)	1.4	3.0	1.6	1.7	2.1	1.4	1.9	1.8	2.1
Width between 1st gill slits (GSW1)	18.1	23.3	18.3	20.1	19.6	19.5	17.5	17.0	18.4
Width between 5th gill slits (GSW2)	no data	15.7	13.0	13.3	12.6	14.1	10.4	10.0	12.5
Snout tip to eye (SnE)	21.0	14.7	18.6	17.5	18.0	19.8	16.9	17.9	20.3
Snout tip to nostril (SnN)	15.5	16.1	15.0	15.1	14.3	16.0	16.4	13.9	16.3
Snout tip to mouth (SnM)	20.4	19.8	18.6	19.8	19.5	19.5	20.4	18.8	20.3
Snout tip to 1st gill slit (SnGS1)	31.4	29.0	30.3	30.7	28.2	32.0	30.0	29.3	31.8
Snout tip to 5th gill slit (SnGS5)	43.5	45.1	42.3	43.7	38.0	42.9	44.3	39.1	42.2
Snout tip to pelvic fin (SnPF)	74.9	80.4	77.6	75.1	71.7	79.8	79.3	71.8	68.7
Snout tip to vent (SnVF)	74.3	83.8	77.3	76.7	74.4	78.5	no data	71.4	74.0
Pectoral fin anterior margin (PFa)	59.0	68.8	60.3	60.4	62.5	60.2	62.3	62.2	60.1
Pectoral fin posterior margin (PFp)	71.1	80.0	69.3	67.4	67.4	73.0	67.7	63.1	69.5
Tail base width (TaW)	6.0	6.1	6.3	4.4	4.5	4.5	5.5	4.5	5.3
Tail length (TaL)	264.3	236.0	272.7	271.7	250.7	312.3	253.1	278.8	174.3

Table 1. Ratios, meristics and colour for *Trygon* (*Himantura*) *oxyrhynchus* (n 116), *Himantura* cf. *oxyrhyncha* (n 116), *Himantura kremplfi* (n 116) and *Himantura uarnak* species complex (n 116), n.e: not erupted; nuc: nuchal series.

	<i>H. oxyrhyncha</i> Holotype MNHN 9639	<i>H. cf. oxyrhyncha</i> MNHN 1923-71 (broken tail)	<i>H. cf. oxyrhyncha</i> MNHN 1986-716	<i>H. kremplfi</i> Syntype MNHN 1922-79	<i>H. kremplfi</i> Syntype MNHN 1922-77	<i>H. kremplfi</i> Syntype MNHN 1922-78 (broken tail)
Meristics						
Total pectoral radials	118	116	116	116	117	112
Prepterygial radials	56	53	54	57	55	53
Mesopterygial radials	15	15	16	15	17	12
Metapterygial radials	47	48	46	44	45	47
Pelvic radials	26	26	18	18	20	19
Vertebral count	34 (114)	37 (109)	33 (112)	39 (119)	32 (112)	39 (114)
Tooth rows upper jaw	41	51	40	32	37	43
Tooth rows lower jaw	45	53	42	?	42	44
Number of middorsal tubercles	41	40	26	2	2	2
Mid-iscapular series	3	2	2	2	2	2
Mid-dorsal truncal series	20	8	4	0	0	0
Mid-dorsal caudal series	18	30	20	0	0	0
Oral papillae	7	8	6	7	7	7
Ratios						
Disc length/preorbital	3.3	3.6	3.7	3.5	3.6	3.8
Disc length/preoral	3.5	3.6	3.5	3.4	3.3	3.5
Disc length/interorbital	9.4	9.6	8.2	8.6	7.5	7.7
Disc length/disc width	1.1	1.1	1.1	1.1	1.1	1.1
Tail length/disc length	2.9	1.2	2.9	2.9	3.0	2.5
Preorbital/interorbital	2.8	2.6	2.2	2.4	2.0	2.0
Preoral/intermarial	3.1	3.2	3.3	3.3	2.9	2.8
Preoral/first gill slits width	1.4	1.4	1.4	1.4	1.4	1.3
Interorbital/eyeball	2.6	2.4	3.1	2.0	2.5	2.0
Preorbital/eyeball	7.3	6.4	7.0	4.9	5.2	4.0
Colour	Lightly reticulated colour pattern	Reticulated colour pattern	Reticulated colour pattern Rounded spots	Dark spots	Dark spots	Dark spots

Table II. – (Continued)

	<i>H. uarnak</i> MNHN 2442	<i>H. uarnak</i> MNHN 1985-208	<i>H. uarnak</i> MNHN A8006	<i>H. uarnak</i> MNHN A8909	<i>H. uarnak</i> MNHN A8909	<i>H. uarnak</i> MNHN A7918	<i>H. uarnak</i> MNHN A7920	<i>H. uarnak</i> MNHN A7921	<i>H. uarnak</i> MNHN A7969 (broken tail)
Meristics									
Total pectoral radials	151	?	145	127	125	152	134	127	142
Proprietary radials	64	?	60	54	51	62	52	52	61
Mesopterygial radials	17	?	20	17	17	18	18	17	15
Metapterygial radials	70	?	65	56	57	72	64	58	66
Pelvic radials	31	?	22	22	22	28	22	24	27
Vertebral count	48 (?)	?(116)	49 (121)	41 (113)	41 (113)	48 (?)	40 (?)	43 (116)	45 (122)
Tooth rows, upper jaw	42	n.e.	32	36	33	34	41	38	42
Tooth rows, lower jaw	46	n.e.	43	45	42	42	48	44	44
Number of middorsal tubercles	2	0	0	0	0	3	7	2	7
Mid-scapular series	2	0	0	0	0	3	3+4 nuc.	2	2+5 nuc.
Mid-dorsal trunk series	0	0	0	0	0	0	0	0	0
Mid-dorsal caudal series	0	0	0	0	0	0	0	0	0
Oral papillae	4	?	4	4	4	4	4	4	4
Ratios									
Disc length/preorbital	4.3	6.1	4.9	5.1	4.9	4.3	5.5	4.6	4.4
Disc length/preoral	4.4	4.6	5.0	4.5	4.5	4.3	4.5	4.4	4.4
Disc length/interorbital	7.1	5.3	7.2	8.1	6.8	6.4	8.3	6.9	6.5
Disc length/disc width	0.9	0.9	0.9	0.9	0.8	0.8	0.9	0.8	0.8
Tail length/disc length	2.8	2.6	2.9	2.9	2.7	3.5	2.6	3.1	1.8
Preorbital/interorbital	1.6	0.8	1.4	1.5	1.3	1.5	1.5	1.5	1.4
Preoral/interanal	2.5	2.2	2.3	2.3	2.2	2.1	2.7	2.0	2.2
Preoral/first gill slits width	1.1	0.8	1.0	0.9	1.0	1.0	1.1	1.1	1.0
Interorbital/eyeball	2.3	2.0	2.2	1.4	1.8	1.8	2.1	2.1	2.5
Preorbital/eyeball	3.7	1.8	3.2	2.2	2.5	2.7	3.1	3.1	3.7
Colour	Dark spots Banded tail	Uniform pale brown	Uniform brown, Dark spots	Uniform brown	Uniform brown	Dark spots, Banded tail	Uniform brown, White spots Banded tail	Uniform brown Banded tail	Uniform brown

internarial width and 1.4 times width between first gill slits. Snout elongated, broad at its base and narrow anteriorly forming a triangle shape. Eyes small, length of eyeball 2.6 (2.4 - 3.1) times in interorbital width and 6.7 (6.4 - 7.0) times in preorbital length. Spiracles large, almost 2 times larger than the eyeball. Nasal curtain with fringed posterior margin. Mouth lightly arched. Upper jaw with 6-7 and lower jaw with 10-11 functional tooth rows, arranged as 41 rows (40-42) on the upper jaw and 45 rows (42-46) on the lower jaw. Teeth arranged in quincunx pavement, similar in upper and lower jaws.

Middorsal surface of disc and tail covered by a dermal armor consisting of numerous heart-shaped denticles and heart-shaped flat tubercles. Dermal denticles of holotype cover mid-dorsal part of disc from preorbital area onto base of tail. Close-set denticles, with flat crown slightly erected and sub-circular basal plate without well differentiated peduncle. Larger heart-shaped denticles sparsely distributed, especially on mid-dorsal area and near the scapular girdle, arranged in incomplete ovoid patch and not extending further onto the pectoral fins. Pectoral fins sparsely covered with very small denticles with stellate bases and blunt crowns, not modified into acuminate tip. Small spiny denticles with stellate basal plate occur on the dorso-lateral sides of the tail, from posterior tip of sting to the tip of the tail, absent in smaller specimens. Ventral side of the disc and tail perfectly smooth, bucco-pharyngeal cavity devoid of any denticle. Mid-scapular area bears two pearl-shaped tubercles (2.5-3.0 mm diameter) with minute cusp on posterior edge. Tubercles pseudo-circular and slightly erected at their posterior edge. Mid-dorsal series composed of 41 heart-shaped and bulbous tubercles in holotype (3 mid-scapular + 20 truncal tubercles + 8 caudal), 26 in specimen MNHN 1986-716 (2 mid-scapular + 12 truncal + 2 caudal) and 40 in specimen MNHN 1923-71 (2 mid-scapular + 18 truncal + 20 caudal). These flat tubercles, are well differentiated from the adjacent dermal denticles and irregularly arranged in a continuous row from the nuchal region to the base of the sting. Sting absent in holotype (scar visible), present in the two other specimens. Floor of the mouth with 6 papillae in two transverse rows (4 anteriorly and 2 posteriorly) and one in the middle located posteriorly to the last row in larger specimens.

Dorsal surface of the disc white with pale brown hexagonal blotches in the holotype. Dermal armor and lateral margins of the disc and pelvic fins are brown, light in holotype, more marked with a reticulated color pattern in other specimens. Smaller specimens patterned with numerous dark blotches of irregular shape, separated by sinuous lines, extending from the mid-length snout-eyeballs to the base of the sting. This color pattern does not extend farther than the mid-width of the dorsal fins. Ventral surface of disc entirely white to pale brown, without any blotch or dark bands.

Distribution

The holotype came from Saigon (Vietnam), and the other specimens come from Cambodia (Pnom Phen and Mekong River). Complementary data given by Smith (1945), Kottelat and Whitten (1996), Compagno (1997), Froese and Pauly (2000), and Last (pers. comm.) indicate that *H. xyrhyncha* is also present in Thailand (Menam Nan river), Sumatra (Sarawak) and Borneo.

Statistical analysis

The combination of the first two principal components accounts for 75.3% of the variance of the morphometric data (55.8 and 19.5% respectively) (Fig. 1) and show that *H. trempfi* and *T. xyrhynchus* are closely related and differ greatly from the *H. barnak* species complex mainly by the shape of the snout (SnM, SnN, SnE), the greater tail base width (TaW) and a lower eyeball (Eb). The character correlations with the two first principal com-

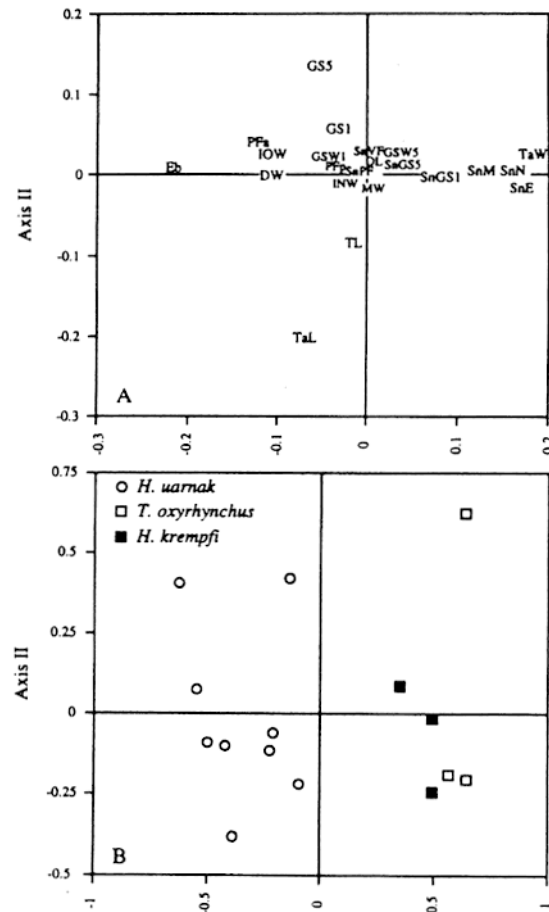


Fig. 1. Factorial plan I and II obtained from a double centred PCA. **A**: Variables; **B**: Individuals. Acronyms are developed in table 1.

Table 1. Character correlations with the two first principal components. Acronyms are developed in table 1.

	DW	TL	DL	Eb	IOW	INW	MW	GS1	GS5	GSW1	GSW5
PC1	-0.07	0.13	0.18	-0.34	-0.07	0.11	0.19	0.09	0.05	0.08	0.22
PC2	-0.06	-0.025	-0.03	-0.04	0.00	-0.06	-0.11	0.07	0.27	-0.02	-0.03

	SnE	SnN	SnM	SnGS1	SnGS5	SnPF	SnVF	PFa	PFp	TaW	TaL
PC1	0.46	0.48	0.43	0.32	0.25	0.15	0.17	-0.10	0.10	0.56	0.01
PC2	-0.08	-0.05	-0.04	-0.06	-0.04	-0.06	-0.01	0.02	-0.04	0.00	-0.50

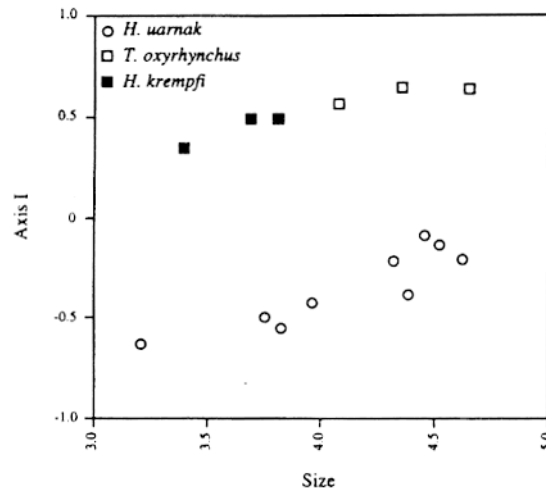


Fig. 3. Relationship between the size and the coordinate on the first axis obtained from a log shape ratio analysis.

ponents are given in table III. The relationship between all variables and the size axis performed on specimens from the group *H. krempfi* and *T. oxyrhynchus* shows some differences mainly in snout characters. But the results of covariance analysis are not significant at $p < 0.01$. However, the size of the individuals of these two groups is different. The relationship between the first canonical axis and the size axis shows clearly the differences between the *H. krempfi* and *T. oxyrhynchus* group and the *H. uarnak* specimens (Fig. 3). The analysis of covariance on the first canonical axis shows that, if *H. uarnak* differs significantly from the other specimens ($p < 0.0001$), *H. krempfi* and *T. oxyrhynchus* are not significantly different. This confirms the hypothesis that specimens named *H. krempfi* and *T. oxyrhynchus* are close to each other morphometrically.

The covariance analysis was performed on the specimens of the *H. uarnak* species complex and on all other specimens considered as only one group using the variables which segregated most of individuals along the first principal component (TaW, SnM, SnN, SnE and Eb) (Fig. 3). The probability for the species by covariate interaction are up to 0.1. So, the assumption of homogeneity of slopes is possible. The tests of intercepts differences for all the five variables are significant ($p < 0.01$). Thus separation along the first axis in the principle component analysis appears to be due to differences in shape rather than differences in developmental rates. A precise comparison by characters follows.

Comparative morphology

Comparisons of the specimens of *Trygon oxyrhynchus* with those of the *H. uarnak* complex and with those of *H. krempfi* show that *T. oxyrhynchus* and *H. krempfi* present the following characteristics (Table IV): total length greater than 430% DW (versus less than 390% DW for *H. uarnak* complex). Disc length 113-117% DW (vs 83-94% DW for *H. uarnak* complex). Internarial width greater than 9% DW (vs 7.3-9.0% DW). Mouth width greater than 9% DW (vs 7.5-9.3% DW). Tail length comprised between 331 and 337% DW (vs 236-312% DW). Width between gill slits greater in *T. oxyrhynchus* and *H. krempfi* than in *H. uarnak* complex (respectively 21.9-22.6% DW, 22.5-24.2% DW and 17.0-23.3% DW for the 1st gill

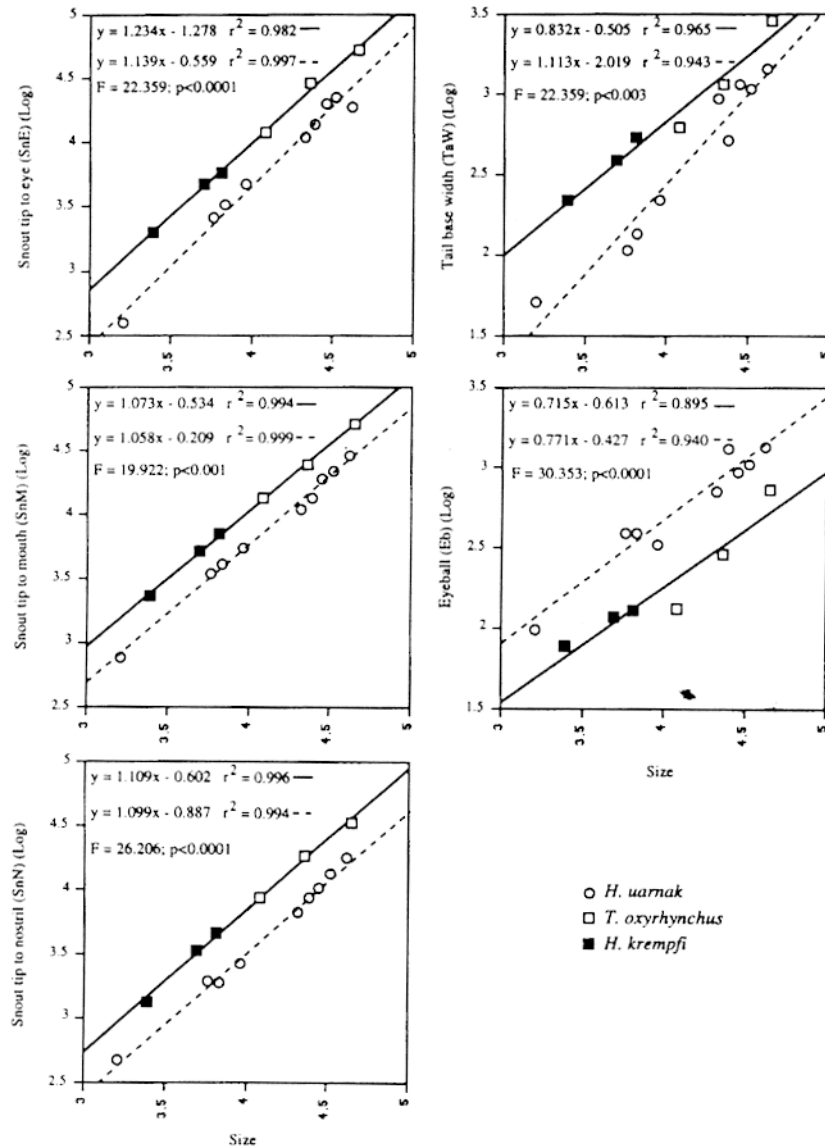


Fig. 3. Log of snout characters, eyeball and tail base width versus log of total length for 15 specimens. F are the values for slope differences.

slits, 16.4-19.3% DW, 16.0-17.7% DW and 10.0-15.7% DW for the 5th gill slits). The following relative distances are larger in *T. oxyrhyncha* and *H. kremphi* than in *H. uarnak* complex: preorbital distance (33.0% DW vs 14.7-21.0% DW), prenasal distance (32.5% DW vs 13.9-16.4% DW), snout tip to 1st gill slit (34.2% DW vs 28.2-32% DW), snout tip to 5th gill slit (32.2% DW vs 38.0-45.1% DW), snout tip to pelvic fin (39.1% DW vs 68.7-80.4% DW), snout tip to vent (39.0% DW vs 71.4-83.8% DW) and tail base width (8.4-11.0% DW vs 4.4-6.3% DW).

Meristics

Meristic values again show a close relationship between *T. oxyrhynchus* and *H. krempfi* (Table II). Total pectoral radials of the studied specimens is between 112 and 118 in *T. oxyrhynchus* and *H. krempfi* versus more than 120 (125-152) in the *H. arnak* complex. The large range of variations in total radial count in the 7 MNHN specimens of the *H. arnak* complex suggests that some specimens previously identified as *H. arnak* could be related to another species.

When separately counted, the number of propterygial (51-64) and mesopterygial radials (12-20) is not significantly different between the species. Metapterygial radials are fewer in *T. oxyrhynchus* and *H. krempfi* (44-48) than in *H. arnak* (56-72). Total vertebral count is similar in *H. arnak* species complex (111-122), *T. oxyrhynchus* (109-114) and *H. krempfi* (112-119), but the number of vertebrae between the second synarcual and the front edge of the pelvic girdle is slightly higher in *H. arnak* species complex (40-49) than in *H. krempfi* (32-39) and *T. oxyrhynchus* (33-37). Upper jaws with 4-7 and lower jaws with 7-11 functional tooth rows are not significantly different within the different specimens. The number of oral papillae depends on the maturity stage of the specimen: 6-7 in two or three rows in *T. oxyrhynchus* and *H. krempfi* (8 mentioned in the specimen MNHN 1923-71 by Compagno and Roberts, 1982), 4 in two rows in *H. arnak* species complex (Annandale, 1909; McEachran and Capapé, 1984).

Ratios

Measurement ratios indicate also a close relationship between *T. oxyrhynchus* and *H. krempfi* (Table II): disc length 3.3-3.8 times preorbital distance (versus 4.3-6.1 in *H. arnak* species complex), 3.3-3.6 times preoral distance (vs 4.3-5.0), 1.1 times disc width (vs 0.9), preorbital distance 2.0-2.8 times interorbital distance (vs 0.8-1.6), preoral distance 2.8-3.3 times internarial distance (vs 2.0-2.7), preoral distance 1.3-1.4 times first gill slits width (vs 0.8-1.1), interorbital distance 2.0-3.1 times eyeball length (vs 1.4-2.5) and preorbital distance 4.0-7.3 times eyeball length (vs 1.8-3.7). The variations observed for this last character between *T. oxyrhynchus* and *H. krempfi* specimens suggest that the length of the snout could be considered as an allometric character with smaller values in juvenile specimens (relative shortness of the snout in juveniles), than in adult specimens.

Colour

Preserved in alcohol, the holotype of *Himantura oxyrhyncha* (= *T. oxyrhynchus*) is almost completely pale brown on the dorsal surface of disc and tail, with a vanishing reticulated pattern of hexagonal spots on the hind part of the disc (Table II). The original description (Sauvage, 1878: 6) indicates «a general grey-brown coloration with several dark spots and mid-dorsal area dark brown with yellow lines forming regular hexagons. Yellow and brown spots on the tail to the level of the spine» (translated from French). In the two other specimens, especially the smaller one (MNHN 1986-716), the colour pattern on most of the dorsal side of the disc, including the base and the hind part of the pectoral fins, is constituted by rounded black spots more or less fused or is reticulated in larger specimens (see fig. 2 in Compagno and Roberts, 1982: 326).

H. krempfi is characterized by a reticulate colour, obscure or absent on the hind part of the disc. The three juvenile specimens of *H. krempfi* are coloured with numerous dark spots over most of the middle part of the disc and the base of the tail. Furthermore, on a same specimen, the different shapes of these spots on the same specimen indicate they vary during ontogeny. The rounded dark spots seem to be characteristic of juveniles specimens and the

reticulate pattern appear only in larger specimens. This kind of reticulated colour pattern also occurs in *H. granulata* (Annandale, 1909, pl. I fig. 3; Compagno and Roberts, 1982: 336; Last, 1994), but most of other species, such as *H. unbricata*, *H. bleekeri*, *H. raco*, *H. thaophraya*, *H. jenkinsii*, *H. tui* or *H. uviatilis* are uniformly colored (Last and Stevens, 1994). Colouration of *H. uarnak* species complex is more variable: some specimens, especially juveniles, are dark spotted or show a reticulated colour pattern (Annandale, 1909; Nakaya, 1984; Last and Stevens, 1994; Sommer *et al.*, 1996), others possess also an uniform brown coloration (Table I), having caused misidentifications for other species (Last and Stevens, 1994).

DISCUSSION

Himantura is composed of about 25 species, most of which occurring in the Indo-Pacific area (Compagno and Roberts, 1982). *Trygon (Himantura) oxyrhynchus* was first considered a valid species, closely related to *Trygon (Himantura) uarnacoides* Bleeker (= *H. uarnak*), but distinguished from this species by the length of the rostrum and the dermal characteristics (Bleeker, reported by Sauvage, 1878: 6). Garman (1913) considered *T. oxyrhynchus* synonymous with *Dasybatus* (= *Himanturus*) *uarnak*, without mentioning the relatively long rostrum and distinct mid-dorsal series of heart-shaped and bulbous tubercles of the specimen. The synonymy of Garman (1913, footnote #1, p.66) was accepted by Bertin (1939), Herre (1953), Fowler (1969), Compagno and Roberts (1982), Kottelat (1984), Séret and McEachran (1986) and Eschmeyer (1998).

In the present study, by comparing the morphological characters, meristic ratios, colour, we clearly show, on the one hand, that *T. oxyrhynchus* can not be considered a synonym of *H. uarnak* and, on the other hand, that it does not differ from *H. krempfi*. Species of the *H. uarnak* complex are well separated from *T. oxyrhynchus* and *H. krempfi* by their diamond shaped disc, the shortness of the rostrum, the colour pattern and meristic counts. The studied specimens of *H. krempfi* are only juveniles and they present some allometry, especially for the head and snout. Our results were confirmed by a log shape ratio analysis (Figs 1, 2). Furthermore, data given by Compagno and Roberts (1982) confirm our observations and meristic counts. *T. oxyrhynchus* can be differentiated from the juveniles of *H. krempfi* by its relative length of the eyeballs (smaller), the mouth width (shorter), the distance from the tip of snout to 5th gill slit (shorter), the length of the snout (more elongated) and the tail base width (less elongated). The number of oral papillae is similar in *T. oxyrhynchus* and *H. krempfi* (6-7 in 2 rows versus 4 in species of the *H. uarnak* complex). *Trygon oxyrhynchus* is set apart from all the other species of *Himantura* by the typical continuous row of heart-shaped and bulbous tubercles extending from the nuchal area to the base of the sting. These tubercles appear in the specimen 185 mm DW and are well developed in sub-adults and adults, their absence in smaller specimens is thus size-related. Garman (1913) did not notice the length of the snout and the continuous mid-dorsal row of tubercles because he had worked on small specimens.

Out of the *H. uarnak* specimens examined, four specimens appear very similar to this species but differ in the number of pectoral radials, colour and morphology. These specimens (MNHN A8909, MNHN A7920 and MNHN A7921) are rather closely related to *Himantura* sp. A Last & Stevens, 1994 and are here considered as *Himantura* cf sp. A until further information.

The biogeographical data indicate that *H. krempfi* is a typical freshwater stingray inhabiting Thailand, Cambodia, Indonesia and Mekong basins (Chabanaud, 1923a, 1923b,

1926a, 1926b; Fowler, 1941; Smith, 1945; Compagno and Roberts, 1982; Monkolprasit, 1985; Kottelat, 1985, 1989; Monkolprasit and Roberts, 1990; Compagno, 1995, 1997; Rainboth, 1996; Eschmeyer, 1998; Taniuchi, 1998; Froese and Pauly, 2000). *Trygon (Himantura) oxyrhynchus* has been collected in the Mekong River, the holotype was reported from Saigon. Three juveniles, identified as *H. bleekeri* by Smith (1945) and as *H. brempfi* by Monkolprasit and Roberts (1990) appear to be juveniles of *T. oxyrhynchus* (see Smith, 1945, pl. 1). These specimens have also been collected in freshwater, in the lower Menam Nan (Thailand). Thus, *H. oxyrhyncha* is regarded here as a freshwater species.

In summary, due to allometric and ontogenic variations between small and larger specimens, also concerning the colour pattern, and regarding the morphometric, ecological and biogeographical data, *Trygon (Himantura) oxyrhynchus* is considered as a valid species of Southeast Asian *Himantura*, named *Himantura oxyrhyncha*. *H. brempfi* could be a junior synonym determined by the rules of priority used in articles N°32 to N°100 of the International Code of Zoological Nomenclature (Eschmeyer, 1990). Regarding the specimens here studied, it appears that the specimens formerly identified as *H. brempfi* (MNHN 1923-71 and MNHN 1986-716), could be considered juveniles of *Himantura oxyrhyncha*. A further investigation of these specimens and a complete study of the various morphotypes within the species *H. barnak* (Annandale, 1909; Last and Stevens, 1994) has to be conducted.

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